

The Association between Vocal Characteristics and Habitat Type in Taiwanese Passerines

JULIA I. SMITH and HON-TSEN YU

*Museum of Vertebrate Zoology and Department of Integrative Biology
University of California, Berkeley, California 94720, U.S.A.*

ABSTRACT—We analyzed the vocalizations of twelve Taiwanese passerines to examine whether vocal characteristics are associated with habitat type: edge, forest canopy, and forest floor. Morton [1] and Richards and Wiley [2] argue that because sound wave propagation is dependent upon the characteristics of the environment, selection should favor the use of song features which will carry information over the required distance [3]. For each vocalization we calculated the frequency emphasized, the range of frequency modulation, and the duration. We found relatively little variation among the members of each species. Vocal comparisons among habitat types revealed that bird sounds of Taiwanese habitats differ. However, in contrast to the pattern found in the neotropics [1, 2, 4], Taiwanese edge species do not emphasize higher frequencies, over a wider range, and with more rapid repetition, than forest dwellers. Most of the vocal differences among habitat types result from forest floor dwelling Taiwanese passerines vocalizing, on average, at frequencies 2000 Hz lower than other species. This supports the hypothesis that, due to the rapid attenuation of high frequency sound near the ground, bird sounds of the forest floor will be of low frequency.

INTRODUCTION

Many researchers [1-4] have argued that the association of certain vocal characteristics with a specific habitat is the result of selection acting to produce a salient signal. Studies of neotropical passerines [1, 2] have demonstrated that forest dwelling species vocalize at lower frequencies, utilize a more restricted range of frequencies, and employ less rapid repetition than birds in open habitats. However, these patterns of vocalization have been documented for some, but not all, North American temperate habitats [4, 5]. Wiley and Richards [4] suggest that behavior may account for vocal differences, between temperate and tropical regions. Specifically, they [4] propose that neotropical forest species, unlike temperate forest passerines, will sing directly from the ground where the effects of attenuation make high frequency sound useless. In addition, Richards and Wiley [2] argue that forest dwelling birds, because of the greater influence of reverberation, may be

more likely to avoid high repetition rates than birds of open habitats. This association of vocal frequency and repetition rate with habitat type has never been examined in Old World tropical Taiwanese passerines. In fact, the vocalizations of the species in our study have never before been analyzed. Therefore, we will describe the basic structure and pattern of vocalization for these twelve Taiwanese passerines and test two hypotheses: 1) whether birds of forested habitats vocalize at lower frequencies and with less variance and slower repetition rates than do birds of open edge areas; and 2) whether birds of the forest floor—subject to the most stringent effects of attenuation—vocalize at lower frequencies than canopy dwellers.

MATERIALS AND METHODS

Recordings were made with a Sony TC-D5M cassette recorder and Sony C-74 microphone. Birds were recorded, in June of 1987, at Wuling (elevation 1800 m) and Chitou (elevation 1200 m) in central Taiwan. The natural vegetation of these two localities is broad-leaf forest dominated by

members of the Fagaceae and Lauraceae [6]. A large portion of the natural forest has been logged and replaced by conifer plantations, primarily *Cryptomeria japonica*. Some birds were recorded along the northeast coast at Yenliao (elevation 50 m); here, *Phyllostachys makinoi* and *Acacia confusa* make-up the secondary growth.

Birds were recorded in two general habitat types: edge and forest. Forest habitat is characterized by two strata. The lower stratum averages 2 m to 8 m high and consists of herbaceous and shrubby plants. The upper stratum, the canopy with many lianas, is about 10 m to 20 m high. The edge areas remain open with grasses (*Miscanthus* spp.) and herbaceous plants.

We studied twelve species of Taiwanese passerines, representing three taxonomic subfamilies—Sylviinae, Timaliinae, and Muscicapinae (Table 1). Based on behavioral observations (H-TY) and behavioral descriptions by DeSchauensee [7], and Hachisuka and Udagwa [8], the species were categorized according to preferred habitat type. For forest dwellers the position they occupy—canopy or floor—was also recorded (Table 1). Vocalizations were analyzed with a Kay Elemetrics 6061B sonograph. Following Morton [1], the frequency emphasized (in Hz) for each sonogram was determined by locating the midpoint of the darkest region of the vocal trace. The extent of frequency modulation in each vocal trace was described by subtracting the minimum from the maximum frequency for each species. For each species, the duration of a typical vocalization was measured to the nearest 0.1 second. Finally, by visual inspection, the occurrence of rapid repetition of similar notes within a vocal trace was noted.

RESULTS

Description of Vocalizations

Edge Species

Liocichla steeri has a vocalization consisting of two loud piercing introductory notes followed by a less emphasized slur, "Dee, deeee-yeer" (Fig. 1a). This vocalization is comprised of very high frequencies—the highest in our study—with exten-

sive frequency modulation (Table 1). Interestingly, the male will duet with the female. The female enters the song during the last syllable of the male's vocalization with a buzzy, "Gee, gee, gee ..." (Fig. 1a). The alteration of voices is precisely timed. It is often difficult to discern that the voices have changed.

Garrulax canorus taewanus, often kept as a cage bird, is renowned for its musical vocalizations. The vocalization consists of clear, rich whistles with an accent on the first note of each doublet or triplet (Fig. 1b). Relative to the other species we examined this vocalization is long and is also highly modulated (Table 1).

Cettia fortipes has a vocalization consisting of a soft hum that crescendos and explodes into a sharp series of notes, "HMMMMMM, switch you!" Extensive frequency modulation (almost 4000 Hz; Table 1, Fig. 1c) occurs in the final elements of the vocalization.

Bradypterus seebohmi vocalizes with a high, thin, rhythmically repeating whistle, "Da, da, deeee, tick." Despite the fact that the entire vocalization covers a wide range of frequencies (almost 3500 Hz; Table 1), no song notes were rapidly modulated; each note of the song is discrete, without any slurring (Fig. 1d). The vocalization is very syncopated.

Forest Canopy Species

Abroscopus albogularis has a vocalization consisting of a high-pitched, extremely rapid repetition of bell-like tinkling notes (Fig. 1e). Of the species investigated, *A. albogularis* exhibits the fastest repetition of notes. It uses very little frequency modulation; within almost one second of vocalization there is less than 1000 Hz of frequency modulation (Table 1).

Niltava vivida produces a lilting series of thin whistled notes (Fig. 1f). It is a relatively long, musical vocalization consisting of much slurred frequency modulation (Table 1).

Heterophasia auricularis uses a loud strident song initiated with several sharply accented notes and ending with a descending slur, "Wheep, wheep, wheep, weeee-oooo." Each note in the vocalization is clear and distinct (Fig. 2a). Each note exhibits extensive frequency modulation, at

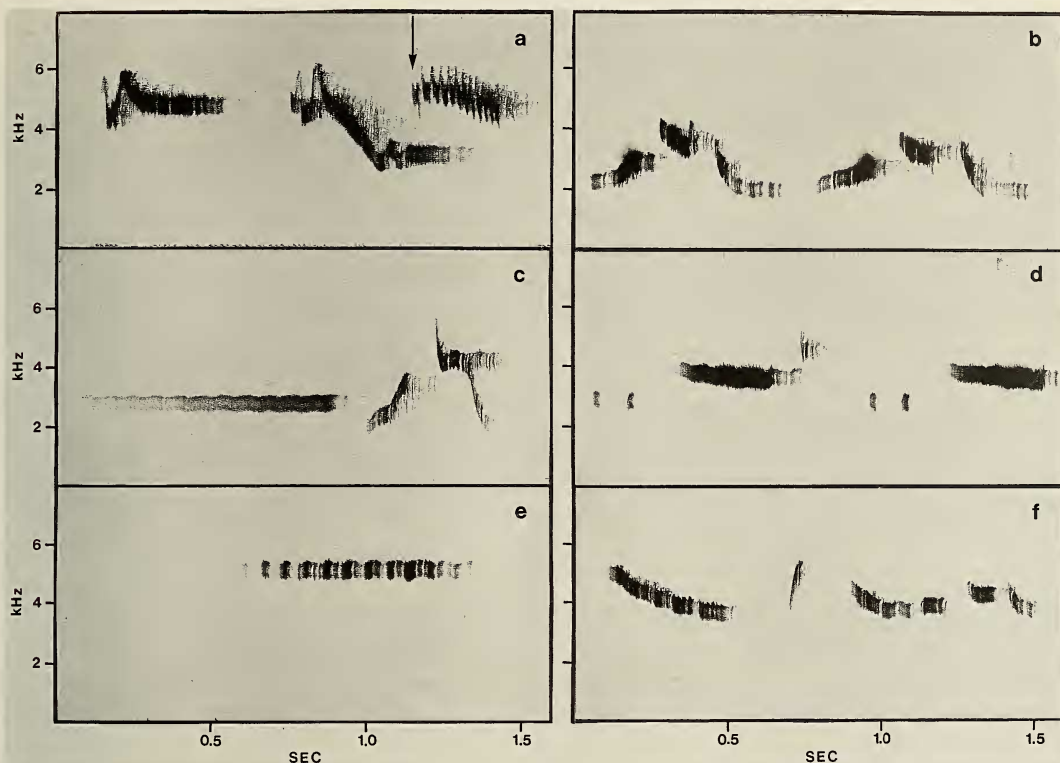


FIG. 1. Sonograms representing the vocalizations of: a) *Liocichla steeri*, the female's vocalization is indicated by an arrow; b) *Garrulax canorus taewanus*, c) *Cettia fortipes*, d) *Bradypterus seebohmi*, e) *Abroscopus albogularis*, and f) *Niltava vivida*.

times as much as 4000 Hz (Table 1).

Yuhina brunneiceps uses a thin, lilting whistle with a descending slur at the end (Fig. 2b). This is musical vocalization. There is a great deal of frequency modulation within and between notes (Table 1).

Forest Floor Species

Pomatorhinus ruficollis musicus vocalizes using an accelerating series of repetitive notes, initiated with an accent, "Duh, doo, doo, doo...Breep." It exhibits very rapid repetition of relatively unmodulated notes (Fig. 2c). Of the species we investigated *P. r. musicus* utilizes the lowest frequencies (Table 1).

Stachyris ruficeps has a vocalization characterized by a very rapid series of clear notes, "Dee, dee, dee" All notes are of the same frequency and about the same sonographic shape (Fig. 2d). The frequency utilized is relatively low and

unmodulated (Table 1).

Garrulax poecilorhynchus uses a very slow, melodic whistle, "Wooo-whip." The frequency of this vocalization is quite low; it never reaches over 2500 Hz (Table 1). The notes are distinctly separated, and the frequency modulation is quite slow (Fig. 2e).

Alcippe brunnea uses a variable series of flute-like notes. It is very musical vocalization. Each note is extensively modulated (Fig. 2f) but within a relatively narrow range of frequencies (typically, not more than 2400 Hz; Table 1).

Habitat Association

Striking vocal differences among species are found within each habitat type (edge, Fig. 1a-d; forest canopy, Fig. 1e-f and Fig. 2a-b; forest floor, Fig. 2c-f). Across all habitat types there are songs which exhibit extensive frequency modulation: edge—*L. steeri* (Fig. 1a), forest canopy—*H. au-*

TABLE 1. The mean vocal frequency (\pm SD), frequency range, and duration of a typical vocalization for each species. Also noted are: habitat type, habitat position, number of individuals analyzed (n), and taxonomic subfamily.

	n	Subfamily	Mean frequency emphasized (Hz)	Frequency range (Hz)	Duration (sec)
Edge					
<i>Liocichla steeri</i>	8	Timaliinae	4524 \pm 302	2186–6470	1.0–1.5
<i>Garrulax canorus taewanus</i>	1	Timaliinae	3322	1661–4022	3.0–6.0
<i>Cettia fortipes</i>	2	Sylviinae	4459 \pm 124	1574–5902	1.2–1.5
<i>Bradypterus seebohmi</i>	2	Sylviinae	3847 \pm 0	2623–5508	0.7–0.8
Mean			4038 \pm 491		
Canopy					
<i>Abroscopus albogularis</i>	3	Sylviinae	4750 \pm 182	4459–5333	0.6–1.0
<i>Niltava vivida</i>	1	Muscicapinae	4327	3235–5246	1.4
<i>Heterophasia auricularis</i>	7	Timaliinae	3485 \pm 239	1486–5333	0.9–1.1
<i>Yuhina brunneiceps</i>	4	Timaliinae	4502 \pm 497	2098–5945	0.7–0.8
Mean			4277 \pm 477		
Forest Floor					
<i>Pomatorhinus ruficollis musicus</i>	3	Timaliinae	787 \pm 87	262–3322	0.8–1.6
<i>Stachyris ruficeps</i>	5	Timaliinae	2203 \pm 39	1749–2448	0.6–1.4
<i>Garrulax poecilorhynchus</i>	1	Timaliinae	1661	1573–2361	0.6
<i>Alcippe brunnea</i>	11	Timaliinae	3091 \pm 280	1574–4197	0.8–1.2
Mean			1936 \pm 837		

auricularis (Fig. 2a), and forest floor—*A. brunnea* (Fig. 2f). Likewise rather unmodulated vocalizations also occur in each habitat: edge—*B. seebohmi* (Fig. 1d), forest canopy—*A. albogularis* Fig. 1e and forest floor—*S. ruficeps* (Fig. 2d). Vocalizations with rapid repetition are found only in forest dwelling species (forest canopy—*A. albogularis*—Fig. 1e and forest floor dwellers—*P. ruficollis musicus* and *S. ruficeps*—Fig. 2c and d). In edge habitat we discovered no rapidly repeating vocalizations (Fig. 1a-d). No apparent structural feature of the vocal traces correlates with habitat type.

Within each species we found relatively little variation in frequency emphasized; standard deviations were never greater than 500 Hz (Table 1). We calculated the mean frequency emphasized, standard deviation, and coefficient of variation (\bar{x} = mean \pm sd, and CV) in each habitat type by averaging the mean frequencies of the species found in that area: edge (n=4, \bar{x} =4038 Hz \pm 491; CV=12.5), forest canopy (n=4, \bar{x} =4277 Hz \pm 477; CV=11.2), and forest floor (n=4, \bar{x} =1936

Hz \pm 837; CV=43.2). Mean frequencies emphasized in each of these habitats differ significantly (Kruskal-Wallis Test $H=7.53$, $df=2$, $P<0.01$; [9]). Frequencies used in the forest canopy are the highest and those of the forest floor are the lowest. Additionally, the mean frequencies used in the three habitats were compared in a pairwise fashion with Dunn's Test [10]. Species from the forest floor use significantly lower frequencies than those of the forest canopy ($Z=2.55$, $0.05<P<0.10$) as well as those of the edge habitat ($Z=2.16$, $0.10<P<0.20$; for this type of comparison Dunn [10] recommends a significance level of $\alpha=0.20$). However, species from the edge habitat utilize frequencies which do not differ significantly from those of the forest canopy ($Z=0.39$, $P>0.20$).

DISCUSSION

In a comparison of edge and forest habitats we found no support for the hypothesis that edge species utilize higher frequencies over a wider range, with more repetition, than all forest dwell-

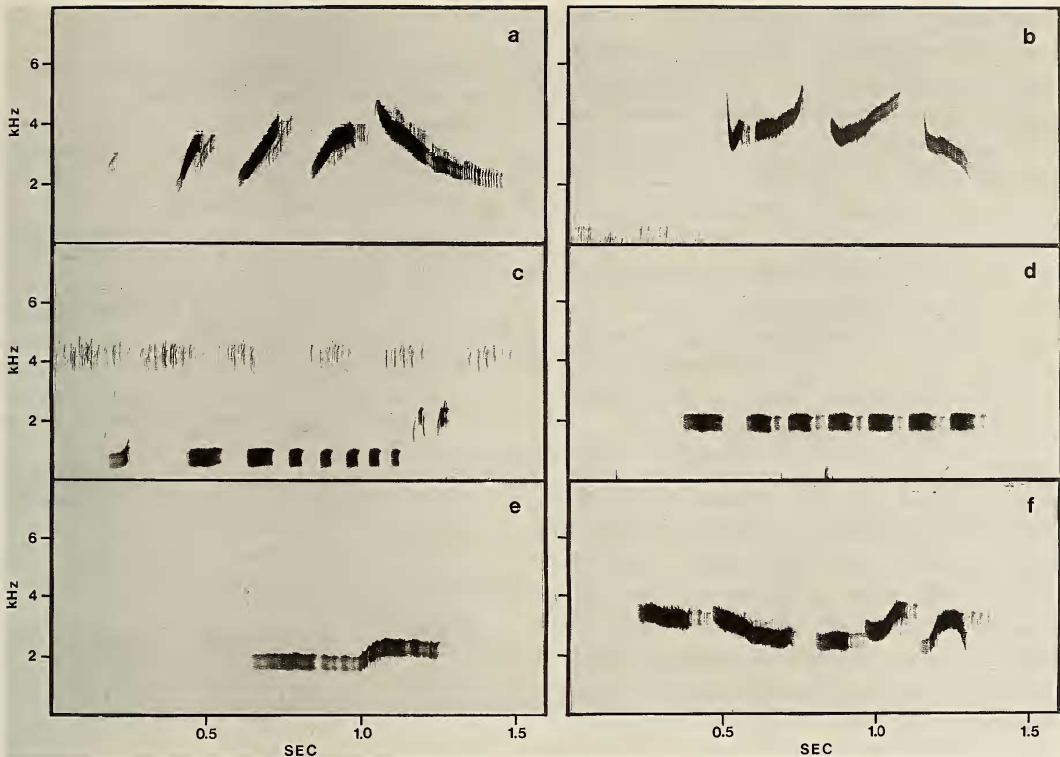


FIG. 2. Sonograms representing the vocalizations of: a) *Heterophasia auricularis*, b) *Yuhina brunneiceps* c) *Pomatorhinus ruficollis musicus*, the vocal trace at 4 kHz is an insect; d) *Stachyris ruficeps*, e) *Garrulax poecilorhynchus*, and f) *Alcippe brunnea*.

lers. Specifically, mean frequencies do differ among the habitats but unlike neotropical passerines the frequencies in edge habitat are only higher than those used by forest floor dwellers not those of the forest canopy. Edge species of the neotropics [1, 2, 4] emphasize a wider range of frequencies than forest dwellers, again a pattern not seen in Old World Taiwanese passerines. The coefficients of variation of mean frequencies emphasized in edge and forest canopy are similar, whereas forest floor dwellers exhibit the greatest extent of variation—the CV is over three times that of the edge species. Contrary to predictions concerning the increased effects of reverberation in the forest on repeated notes [2], we found that Taiwanese edge species do not use more rapid repetition rates than forest dwellers. In fact, of the edge species we investigated (Fig. 1a-d) none utilized a repetition rate greater than the forest canopy dweller *A. albogularis* (Fig. 1e). In addi-

tion, two of the four forest floor dwellers (*P. r. musicus* and *S. ruficeps*) utilize extremely rapid repetition (Fig. 2c and 2d). Again the pattern exhibited by Taiwanese (Old World tropical) passerines is not that of their neotropical counterparts. Interestingly, Handford [11] and Nottebohm [12] both report, from analyses of within species variation in *Zonotrichia capensis*, that some differences among dialects do not match Morton's [1] predictions. They [11, 12] speculate that there are features of a habitat, other than the physical milieu, that can influence the structure of song and thus vocal patterns can contradict Morton's [1] predictions. Perhaps in the Old World tropics some aspects of avian vocalizations are not only modified by the physical environment but also by the vocalizations of other species.

The most striking vocal difference among Taiwanese passerines is found in the frequencies used by forest floor dwellers. These frequencies

are, on average, 2000 Hz lower than those of the canopy and edge dwellers. This pattern cannot be explained by phylogeny whereby phylogenetic constraints result in the most closely related species occupying the same habitat and utilizing the same vocal frequencies. Within each habitat type more than one subfamily is represented (Table 1). Indeed, the two most closely related species in the study—the *Garrulax* congeners—occupy different habitat types and vocalize at very different frequencies (Table 1). Thus, there is support for the hypothesis that, due to the rapid attenuation of high frequency sound near the ground, bird vocalizations of the forest floor tend to be of low frequency.

In conclusion, our data do not support the hypothesis that tropical edge species vocalize at higher frequencies, with more rapid repetition, and with a wider range of frequencies than forest dwellers. However, our data do support the hypothesis that vocalizations of forest floor dwelling passerines may be influenced by the acoustic properties of their environment.

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REFERENCES

- 1 Morton, E. S. (1975) Ecological sources of selection on avian sounds. *Amer. Natur.* **109**: 17–34.
- 2 Richards, D. G. and Wiley, R. H. (1980) Reverberations and amplitude fluctuations in the propagation of sound in a forest: implications for animal communication. *Amer. Natur.* **115**: 381–399.
- 3 Nottebohm, F. (1985) Sound transmission, signal salience, and song dialects. *Behav. Brain Sciences* **8**: 112–113.
- 4 Wiley, R. H. and Richards, D. G. (1982) Adaptation for acoustic communication in birds: Sound transmission and signal detection. In "Acoustic communication in birds". Ed. by D. E. Kroodsma and E. H. Miller, Academic Press, Inc. New York, Vol. 1, pp. 131–181.
- 5 Wasserman, F. E. (1979) The relationship between habitat and song in the white-throated sparrow. *Condor* **81**: 424–426.
- 6 Li, H. L., Liu, T. S., Huang, T. C., Koyama, T. and DeVol, C.E. (1975) *Flora of Taiwan*. Vol. 1. Taipei, Epoch Publishing Corp.
- 7 DeSchaunsee, R. M. (1984) *The birds of China*. Washington, D. C., Smithsonian Institution Press.
- 8 Hachisuka, M. and Udagwa, T. (1951) Contributions to the ornithology of Formosa. *Quart. J. Taiwan Museum* **4**: 1–180.
- 9 Sokal, R. R. and Rohlf, F. J. (1981) *Biometry*. 2nd ed. San Francisco, W. H. Freeman and Company.
- 10 Dunn, O. J. (1964) Multiple comparisons using rank sums. *Technometrics* **6**: 241–252.
- 11 Handford, P. (1981) Vegetational correlates of variation in the song of *Zonotrichia capensis*. *Behav. Ecol. and Sociobiol.* **8**: 203–206.
- 12 Nottebohm, F. (1975) Continental patterns of song variability in *Zonotrichia capensis*: some possible ecological correlates. *Amer. Natur.* **109**: 605–624.